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Distyly supergenes as a model to understand the evolution of genetic architecture.

Genetic architecture, the relative positions of genes across the genome, can appear random with genes scattered without regard to function, but evidence suggests that it is shaped by evolution. In particular, the evolutionary trajectories of functional traits can both be influenced by and influence their underlying genetic architecture. Where multiple loci contribute to local adaptation, coadapted gene complexes can form that consist of combinations of alleles whose interactions have been shaped by selection to optimize trait expression (Prakash and Lewontin, 1968; Allard et al., 1972).

Coadapted gene complexes, however, are vulnerable to disruption by recombination following gene flow from outside the zone of local adaptation if different zones have distinct sets of alleles. The power of recombination to disrupt allelic combinations is reduced if loci are situated in close physical proximity to each other in the genome. Models of the evolution of genetic architecture show that divergent gene clusters can emerge under selection with gene movement and turnover across the genome (Yeaman, 2013; Lindke and Buerkle, 2015). A growing body of empirical evidence of clustered genomic architectures underlying adaptive traits supports these ideas (Table 1). The extent to which adaptation avails of pre-existing genetic architecture or whether genetic architecture evolves in response to selective pressure is an open question, however. Answers will come from systems where the genetic architecture underlying an adaptive trait has important consequences for expression and function.

The supergenes that control expression of distyly are a compelling example of the importance of genetic architecture for the expression and evolution of an adaptive trait. Distyly is a floral polymorphism with two floral morphs. Tristylous species with three floral morphs are also known but the extra complexity of tristylous systems is not considered further in this essay. In distyly, the stigma and anthers are separated by length differences within flowers but the length differences are switched in the other floral morph. These floral organ length differences favour reciprocal pollen transfer between morphs, thereby promoting disassortative pollen transfer and reducing pollen wastage (Lloyd and Webb, 1992). In addition to the minimum requirement of different style and filament lengths, or reciprocal herkogamy, in each floral morph, the distylous flowers often also show intra-morph-incompatibility and differing ancillary pollen and stigma characteristics (Lloyd and Webb, 1992).

Classical genetic studies across several species show distyly to be under the simple genetic control of a single diallelic locus (Charlesworth and Charlesworth, 1979; Barrett and Shore, 2008). The two alleles interact in a dominant-recessive manner so that heterozygous individuals express one flower morph and recessive allele homozygotes express the other morph. This mode of inheritance insures that inter-morph crosses will generate equal morph proportions of progeny as favoured by negative frequency-dependent selection to maximise mate availability. This simple genetic basis disguises an interesting genetic conundrum: how can a single locus be responsible for the multiple distinct floral traits that typically distinguish the different floral morphs? This is solved by the presence of a supergene consisting of multiple highly-linked genes with morph specific alleles enabling the multiple traits comprising each floral morph to be inherited as a single unit (Charlesworth 2016). Large non-recombining regions at supergenes have been identified in some distylous species (> 610 kb in *F. esculentum*; Yasui et al., 2012, 278 kb in *P. vulgaris*; Li et al., 2016).

Far from being an evolutionary curiosity, the phylogenetic distribution of distyly suggests as many as 28 independent evolutionary origins. Corroborating this, different candidate genes for distyly have been identified in different plant families. Five genes: *GLO^T, CYP^T, CCM^T, PUM^T and KFB^T*, have been identified at the newly sequenced *Primula vulgaris S* locus (Li et al., 2016; see also Nowak et al., 2015; Huu et al. 2016). Of these genes, *GLO^T CYP^T* have been found to control anther position and style length, respectively. Other candidate genes have been identified in distylous species from other plant families: *TSS1* in *Linum grandiflorum* (Linaceae; Ushijima et al., 2012), *S-ELF3* in *Fagopyrum esculentum* (Polygonaceae; Yasui et al., 2012), and *TsSPH1* in *Turnera sublata* (Turneraceae; Labonne and Shore, 2011).

Genetic architecture therefore plays a central role in the expression and function of distyly, but how does it evolve? Two alternative evolutionary scenarios are possible. Scenario 1: A pre-existing genetic configuration facilitates the evolution of distyly. The minimum requirements for the establishment of a distyly supergene involve the chance co-location of two loci influencing style and filament length respectively. Selection against recombination between this pair of loci could lead to a supergene zone of low recombination, "trapping" neighbouring loci that could then be recruited to further refine floral form. Scenario 2: Genetic architecture evolves subsequent to the establishment of distyly. In this scenario, the recruitment of genes by translocation into the supergene zone allows the evolution of increasingly complex floral polymorphisms to maximise the efficiency of cross-pollination. Empirical evidence supporting scenario 1 comes from the analogous situation of the gradual expansion of sex determining regions and sex chromosomes through the suppression of recombination (Charlesworth 2016) and co-segregation of functionally unrelated traits such as the *hose in hose* and *oakleaf* mutants reported for *P. vulgaris* (Li et al., 2016). However, as floral polymorphisms become increasingly elaborate, it seems unlikely that all the functional loci involved owe their presence to chance juxtaposition prior to the evolution of distyly.

The near future of heterostyly research will look beyond identifying individual loci underlying different floral morph phenotypes in individual species and their close relatives and will move towards characterizing the entire supergene structure of distylous species from multiple independent origins. Within-family analyses will be able to track the evolution of supergene structure itself by determining the order in which genes are recruited to distyly function (Figure 1). Scenario 1 will be supported if the S locus genes contributing to distyly are also physically close in outgroup taxa that diverged before the origin of distyly. Scenario 2 will be supported if more derived family members show progressively more S locus genes than more basal members and that these genes were recruited to distyly function through translocation.

Plant mating systems frequently transition from outcrossing to selfing, which in this case involves reversion of distyly to homostyly (Barrett and Shore, 2005). Several examples of loss of distyly will likely be present in large taxonomic samples (Sakai and Wright, 2008; McDill et al., 2009). Study of these transitions and the subsequent decay of supergenes will provide insight into the selective forces that once maintained supergene architecture. Loss of gene function, resumption of recombination, and supergene restructuring are some of the potential outcomes following loss of distyly. But which of these processes is the typical initial trigger for loss of distyly?

The study of distyly across multiple evolutionary scales will be invaluable to our understanding of the evolution of co-adapted genomic islands more generally. Independently evolved distyly systems

represent independent evolutionary experiments that can be compared and contrasted. Large genera with a mix of homostylous and distylous species such as *Psychotria* (Rubiaceae) might be useful for such studies (Sakai and Wright, 2008), while herbaceous genera such as *Primula* or *Turnera* are more experimentally tractable. Between-family comparisons would provide insights into general mechanisms by which recombination is locally suppressed and allelic dominance achieved. Intriguingly, recent findings in *Turnera* and *Primula* indicate that distyly genes are hemizygous with different morph types resulting from the presence or absence of a single supergene haplotype (Labonne and Shore, 2011; Nowak et al., 2015; Li et al., 2016). A single morph-specific supergene haplotype solves both the problem of recombination between different morph supergenes and the control of dominance interactions; the dominant phenotype being conferred by supergene presence. It remains to be seen how general a solution to distyly genetic architecture this might be.

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144 Table 1. Adaptions influenced by their underlying genetic architecture.

Genetic architecture	Example
Functionally linked gene cluster	Some diterpenoid and triterpenoid biosynthetic pathways in rice (Swaminathan et al. 2009)
Chromosomal rearrangement	Ecologically distinct parent and hybrid species in sunflowers (Reiseberg et al., 1995)
Chromosomal inversion	Life history and ecological differences in monkeyflowers (Twyford and Friedman, 2015)
Sex determining chromosome/region	Dioecy, separate male and female individuals in campion (Bergero and Charlesworth, 2011)
Centromeric region	Sexual spores containing both mating types in anther smut fungus (Hood and Antonovics, 2004)

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Figure 1. Distyly evolution involves the recruitment of linked genetic loci to a non-recombining supergene. Legend. Black lines depict evolutionary diversification within a family resulting in species A to G at the tips of the phylogenetic tree. Coloured images represent floral structure in each species with blue representing petals, yellows and oranges representing stamens and pollen, and greens representing pistils. Letters along the phylogenetic tree branches represent genetic loci involved in the distyly phenotype. Species A shows an ancestral homostylous phenotype. Species B shows an approach herkogamy polymorphism with differences in female (*F*) organ length. Species C shows with additional reciprocal changes in male (*M*) organ length. Additional elaborations to distyly are then possible such as self-morph incompatibility (species D; gene *I*), pollen size (species E; gene *P*), and floral organ repositioning (species F; gene *R*). These traits could evolve in any order but their controlling loci must be linked to the supergene to be associated with distyly. Species G indicates that evolution is not necessarily directional and distyly can also be lost.